# On the Mouth-Parts and Mechanism of Suction in *Schizoneura lanigera*, Hausmann.

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(PLATES 24 & 25, and 2 Text-figures.)

[Read 5th February, 1914.]

## I. INTRODUCTORY REMARKS.

OWING to the great importance of the family Aphididæ from the point of view of Economic Entomology, it is thought that a detailed investigation of the structure and mechanism of the mouth-parts and associated structures in a member of this family, may be of considerable help in elucidating many points in connection with the life-history and habits of these insects.

There are many questions associated with the mechanism of suction in Aphids, about which our knowledge is very obscure. The action of the stylets in the plant tissues is by no means clearly understood, although Büsgen (1890) contributed a great deal to our knowledge of this problem.

When considering the influence of the sap of certain plants upon the development and reproduction of Aphids, it is very essential to know exactly from which cells the necessary food is derived. There is moreover the question as to why certain species of Aphids produce galls on the host plants, as is the case with the species under consideration.

From observations made in connection with some experiments I have carried out this summer, it seems evident that these insects are susceptible to changing conditions of growth of the host plant. The present paper has been written in the hope that it may be helpful in the further investigations of the problems mentioned above. It deals only with the anatomy of the mouth-parts and associated structures, and attempts to give a clear account of the way in which the plant juices are conveyed into the pharynx and then passed through the œsophagus into the stomach, and further to explain how the secretion from the salivary glands is forced by the salivary pump into the tissues of the host plant.

This work has been carried out in the zoological laboratory of the Royal College of Science, London, where the author has been working for the past year as a Board of Agriculture Research Scholar. Through the kindness of Mr. P. Awati, who has been investigating the mouth-parts of *Lygus pabulinus*, Linn., I have been able to examine his sections, and the comparative observations have been most helpful. Mr. Awati is shortly publishing his paper on *Lygus*. The reader is referred to a previous paper by the author on the general anatomy of *Schizoneura lanigera*, which gives a more general description of the alimentary canal and associated structures, and should be read in conjunction with this paper.

I should like to take this opportunity of expressing my sincere thanks to Professor Maxwell Lefroy for the many suggestions and advice he has kindly given me during the progress of the work, and also to Mr. Clifford Dobell for much valuable assistance in connection with methods of technique and references to literature.

## II. Technique and Methods.

Specimens were fixed in Carnoy's fluid and kept in 90 per cent. alcohol. Bouin's picro-formal mixture was also used.

The mode of preparation of material for the paraffin bath was as follows. After passing through the alcohols to absolute alcohol, the material was placed in chloroform for several hours, then in a mixture of equal parts of chloroform and wax and finally in the paraffin bath. Paraffin-wax melting at 58° C. was used and the best results were obtained when the material was left in the bath for about two hours. Only the head was imbedded, but for entire specimens a longer time in the bath is advisable. Sections were cut from 4–10 $\mu$ thick, in three planes, transverse, vertical, and longitudinal.

Normal saline solution, glycerine, and turpineol have been used as examination media.

For examination of cleared specimens the material was taken through alcohol and cleared in cedar-wood oil, clove-oil, or turpineol, and mounted in alcoholic or xylol balsam.

Sections were stained with hæmatoxylin (Ehrlich) and orange G or eosin.

For examination of the chitinous parts the material was treated with 10 per cent. potash for several hours and then washed in slightly acidulated distilled water and examined in pure glycerine, or mounted permanently in the usual way in Canada balsam.

The drawings were made from Camera lucida sketches, and owing to the minute detail of the parts very high magnifications were necessary, so that most of the work was done with a $\frac{1}{12}$ oil-immersion lens, and in the case of figs. 4–14 and fig. 24 a No. 18 occulo was used.

## III. Nomenclature; Review of Literature.

The terms used throughout this paper are based solely upon the study of the anatomy, and do not necessarily imply a definite homology with other Hemiptera. It is not intended to discuss in any detail the homologies and morphology of the different parts. As far as possible established names have been given, but generally speaking the terms are mainly used for convenience of description.

Most of the published work dealing with the mouth-parts of Hemiptera is confined to the division Heteroptera. The deflexed position of the head in the Homoptera gives rise to several structural differences between the two divisions.

The description throughout refers to the head in the feeding position, so that the clypeal or dorsal face of the *fore-head* is spoken of as the anterior or dorsal face, and the surface which is adpressed to the venter in repose, as the posterior or ventral face*. The distal end of the fore-head is towards the extremity of the labrum and the proximal end towards the epicranial region of the head.

Several of the earlier anatomists, for instance Westwood and Burmeister, tried to homologise the mouth-parts of sucking insects with those of the mandibulate or biting insects, and in 1853 Gerstfeld published a paper dealing specially with the mouth-parts of sucking insects. Geise (1883) published a paper on the mouth-parts of *Notonecta, Nepa*, and *Corixa*, and described the salivary pump (Wanzenspritze) which Mayer had described in *Pyrrhocoris apterus* in 1874. Wedde (1885) dealt with the mouth-parts of some Rhynchota and made some observations on the method of suction. Two years later Leon (1887) studied *Pentatoma*, and made observations on the homologies of the parts. The next important paper is that of Heymons (1899), who made many interesting additions to our knowledge of the morphology of the Hemipterous trophi. The most valuable contribution within the last few years is that of Bugnion and Popoff (1911). These authors have dealt specially with *Graphosoma lineatum*, but have also studied several other species of Heteroptera. In an introductory chapter they give many of the different views held by previous workers, as to the homology of the different parts of the trophi.

So far as the Homoptera are concerned very little work has been done. Smith (1892) attempted to homologise the mouth-parts of *Cicada* with those of Diptera, but his work was much criticised by Marlatt (1895). In 1898 Smith published a further paper upholding his views that the proboscis and stylets are maxillary structures, and that no trace of mandibular structures occur in any present form of Hemiptera.

Meek (1913) published an important work on the mouth-parts of *Cicada septendecim*, in which he shows the close relationship existing between the structure of the head and trophi in this Homopterous insect and the many Heteropterous insects that have been studied. He also gave an account of the method of suction. During the past two or three years Muir and Kershaw have made some interesting additions to our knowledge of the morphology of the mouth-parts in Heteroptera and Homoptera. Their conclusions are based chiefly on the study of the development of the embryo of *Pristhesancus papuensis* and of *Siphanta*. They have also made a general comparative study of different families, and have endeavoured to show

* *Vide* footnote on p. 311.

the close relationship that exists between the trophi of Heteroptera and Homoptera.

To supplement this brief review of the literature I shall indicate as far as possible, the relationships which the mouth-parts herein described bear to those studied in other Hemiptera.

The salivary pump is the "Wanzenspritze" noted by Landois (1868) in *Cimex lectularius*. A few years later it was described by Mayer (1874) in *Pyrrhocoris apterus*, and since then, from time to time, by many authors in different species of Hemiptera, including Aphids and Coccids. Muir and Kershaw (1911 *b*) consider that the salivary pump arises as a modified development of the salivary duct.

The morphology of the sclerites forming the head is a much debated question. Owing to the deflexed position of the head in Homoptera the distal part forms a freely articulating chitinous capsule which supports the trophi. This, which is the Vorderkopf of many German authors, I propose to call the *fore-head*. Meek (1903) has described the *fore-head* in *Cicada* as made up of the frons, clypeus, labrum, epipharynx, and the mandibular and maxillary sclerites. The tapering upper lip, which I call the labrum, appears to be the part referred to by Meek as the prolongation of the epipharynx; the labrum he considers as being considerably reduced.

This view is also held by Muir and Kershaw (1911). It will be seen later that I retain the name epipharynx for the specially thick chitinous roof of the pharyngeal duct, which also forms the floor of the part I call the clypeo-labrum.

The structure I refer to as the clypeus corresponds in position to the frons of Meek in *Cicada*. A slight transverse depression divides it off from the clypeo-labrum, but internally it is defined by the presence of the pharyngeal struts, which are really thickened parts of the clypeal folds. The clypeus supports the divaricator muscles of the pharynx.

There is some doubt as to the parts which make up the labium. Geise (1883) considers it as the lower lip. Léon (1887) described rudimentary labial palps in *Hydrocores*; but Heymons (1899) found, by studying the development in the embryo, that the proboscis is formed by the fusion of a simple pair of appendages (2nd maxillæ), which bear no trace of palps. He considers these latter structures arise as secondary developments. Muir and Kershaw (1911) have shown that the proboscis is formed by the fusion of the simple 2nd maxillæ, and afterwards becomes secondarily divided into segments; they found no clue to the missing palps.

The morphology of the stylets is a much debated point. Originally it was thought that they represented the maxillæ and mandibles. Smith (1892) drew attention to the fact that certain sclerites, which formed part of the chitinous capsule of the *fore-head*, were really associated during development with the stylets, so that the stylets do not really represent the complete mandibles and maxillæ.

Heymons (1896–8) showed from embryology that the internal or posterior stylets represent only part of the first maxillæ. During development the basal portion of each maxilla forms a chitinous plate, which fuses with the wall of the head. The work of Muir and Kershaw (1911) has confirmed this both in Homoptera and Heteroptera ; hence this pair of stylets I have called the maxillary stylets, and their sclerites the maxillary sclerites.

Bugnion and Popoff (1911) consider the anterior or dorsal pair of stylets also represent only part of the mandibles in Heteroptera, the basal portion of the mandible forming a sclerite which fuses with the wall of the head.

Meek also considers that mandibular sclerites (loræ) are present in *Cicada*. The later work of Muir and Kershaw (1911–12) on the embryology of *Pristhesancus papuensis* and *Siphanta* shows that the mandibular sclerites (so-called) have no relation to these stylets, and are not derived from them, and thus I call these stylets the mandibles. The structures I refer to as the clypeal sclerites agree in position with the loræ or mandibular sclerites of Meek.

## IV. Anatomy of the Head and Mouth-parts.

### A. *External Structure.*

The *head* in repose is strongly deflexed beneath the anterior end of the body. On examination of its anterior face, it is seen to be divided into two distinct portions by a transverse suture, situated near the vertex. The proximal portion, which bears the eyes and antennæ, comprises the *epicranial region*. The distal portion is conical in shape and tapers distally, forming a stout, chitinous capsule which supports the trophi. For purposes of description I shall refer to the structure as the *fore-head* *. It freely articulates with the epicranial region by means of thin, flexible chitin (Pl. 24. fig. 1, *a.f.*), which allows freedom of movement, enabling it to be raised or deflexed at will.

The epicranial region is broad and convex and is continuous at its proximal end with the prothorax.

The fore-head is strongly convex on its anterior and antero-lateral faces, and is composed of several chitinous plates or sclerites.

The post-lateral walls, *vide* fig. 18 (Pl. 25), are flat and composed of thinner chitin.

In the distal half of the fore-head the integument folds into the interior, between the sclerites, forming well-defined chitinous folds, as indicated in text-fig. 1.

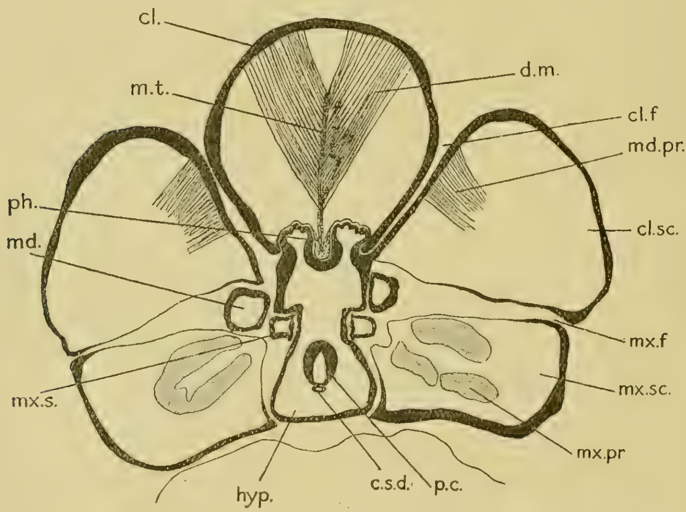
Looked at from its anterior face, the fore-head is seen to consist of dome-shaped areas, *vide* fig. 1.

* In a previous paper I called this structure the frons. This term is misleading. It is the Vorderkopf of many German authors and for want of a better word I use the literal translation *fore-head*.

A large median plate, which I call the *clypeus, cl.*, extends from the proximal margin of the fore-head and forms the greater part of the anterior face. Distally it narrows somewhat, and is divided by a shallow, transverse depression from a smaller triangular sclerite, *cl.l.* This I call the *clypeo-labrum.* It seems to be really a continuation of the clypeus. A tapering plate of chitin, the *labrum, lbr.*, extends in the median line from the distal end of the clypeo-labrum.

The floor of the clypeo-labrum, Pl. **24.** fig. 1, *e.p.*, is composed of thick chitin, which forms the roof of the pharyngeal duct, *ph.d.* This is the *epipharynx.* It possesses a deep, longitudinal groove on its internal face,

Text-fig. 1.




Transverse section through the fore-head in region of pharynx protuberances, showing relation of sclerites forming the fore-head. ×300.

(For explanation of lettering see p. 329.)

as is shown in transverse sections, figs. 7–9, which affords a support for the maxillary stylets.

Distally, it is continuous with the internal face of the labrum, but the chitin becomes much thinner.

The labrum possesses a few, small, transverse ridges on its outer face and a longitudinal groove on the internal face. It is connected with the clypeo-labrum by a thin chitinous fold, which permits free movement.

Two folds of chitin, the *clypeal folds*, text-fig. 1, *cl.f.*, extend into the fore-head on each side of the clypeus, and become continuous with the dorsal wall of the pharynx.

At the anterior end of the pharynx the walls of the fold are composed of very stout chitin and form two strong chitinous struts, the *pharyngeal struts* (*ph.st.*, figs. 13 & 14), which extend to the antero-lateral walls of that structure, affording a firm support for it. The clypeal folds separate the clypeus from two lateral sclerites, the *clypeal sclerites, cl.sc.* (mandibular sclerites or loræ of some authors).

Two *maxillary sclerites*, *mx.sc.*, are situated below the clypeal sclerites, and help to form the latero-ventral walls of the fore-head. They extend ventrally towards the mid-ventral line. In the post-ventral region they merge into the floor of the fore-head which is composed of thin chitin, fig. 18, *f.h.*

Distally, the maxillary sclerites lie close together in the mid-ventral line and extend beneath the clypeo-labrum and labrum. They are separated for some distance, however, by a median plate of chitin which merges proximally into the ventral wall of the fore-head. This is the *hypopharynx*, *hyp.* It is continued forward beneath the *pharyngeal duct, ph.d.*, as a small *hypopharynx lip*, *hyp.l.*, fig. 1. The maxillary sclerites, closely apposed in the median line, extend beneath the hypopharynx lip, concealing it from the ventral aspect, and form two tapering processes, the *maxillary processes* as seen in sections, figs. 4–7, and shown in fig. 2, *mxp.*

The maxillary sclerites turn inwards on each side of the hypopharynx and form two deep folds, the *buccal folds, b.f.* These folds remain open throughout and form two large cavities or chambers, the *buccal cavity*, *b.c.*, which accommodate the stylets. Towards the distal end, the internal faces of the maxillary sclerites and maxillary processes are composed of stout chitin, and ar grooved, thus affording support for the stylets, figs. 6–8.

The hypopharynx lip extends beneath the pharyngeal duct, forming the ventral wall of that structure. Proximally the lip dips down and becomes continuous with the broader portion of the hypopharynx, *hyp.* A large bay is thus formed in which the *salivary pump*, text-fig. 2, *s.p.*, is situated, being attached to the wall of the hypopharynx by means of a stout chitinous supporting base, figs. 2, 12, 13, and 23, *p.s.*

The *salivary pump* can be seen through the integument in cleared specimens as a dark "ᛘ"-shaped chitinous structure.

The floor of the fore-head, into which the hypopharynx merges at its proximal end, becomes continuous with the dorsal wall of the *proboscis* or *labium*, fig. 1, *lbm.*, and text-fig. 2 (p. 325). This latter structure turns beneath the hypopharynx, and at its proximal end its walls consist of thin, flexible chitin.

The post-lateral walls of the fore-head are composed of thinner chitin, fig. 18, *l.w.* When viewed from the anterior or dorsal face, in cleared specimens, there appears to be a ridge of chitin running along the lateral edges of the clypeus. This however, is due to the thick chitin of the clypeus joining on to the thinner lateral walls of the fore-head.

The clypeal sclerites and maxillary sclerites are separated by the *maxillary folds*, *mx.f.* These represent the mandibular folds of Muir and Kershaw. As in the case of the clypeal folds, the in-turned edges of the maxillary and clypeal sclerites are held firmly together by connective tissue. In sections the connective tissue tears away and the sclerites become separated. The maxillary and clypeal folds extend towards the proximal end of the fore-head, where the sclerites merge together to form its lateral walls.

The internal, lateral walls of the hypopharynx (figs. 11–14) are composed of stout chitin and become continuous with the wall of the pharynx, forming part of the stout chitinous supports which surround its anterior end. The pharynx is held firmly in position by these supports, *vide* fig. 14.

B. *The Endoskeleton of the Head.*

The *endoskeleton of the head* consists of strong, hollow, chitinous bars, formed by invaginations of the integument of the head. These bars, which form the arms of the tentorium, give support to the fore-head, and also afford attachment for several muscles. Figs. 2 and 3 show the chitinous endoskeleton as seen in potash preparations of the head.

The arms of the tentorium expand at their extremities and form a broad, hollow, *transverse plate*, *t.p.*, which is situated in the posterior region of the head, beneath the supra-œsophageal ganglion, and forms the central support of the tentorium. The antero-dorsal arms, the antero-ventral arms, and the ventral rods *, are attached or continuous with the transverse plate. The chitin of this latter structure is thinner towards the middle, but becomes much stronger towards its ends, from whence the tentorial arms pass.

The *antero-dorsal arms*, *a.d.*, are formed by two invaginations at the posterior end of the clypeal region of the head. They extend in a posterior direction to the transverse plate, fig. 3, *a.d.*

The *antero-ventral arms*, *a.v.*, pass forward ventrally, diverging from one another, towards the infra-posterior angles of the fore-head. Each then bends upwards, along the lateral wall, and ends at the proximal end of the maxillary fold. From this region a stout triangular bar of chitin passes into the fore-head from each side, which form two levers, *md.l.*, for the dorsal or anterior pair of stylets (mandibles). The position of these levers corresponds to the position of the ends of the maxillary folds, and each lever appears to be a thickening of the fold in this region, fig. 16, *md.l.*, being part of the clypeal sclerite.

The *ventral chitinous rods*, *v.r.*, fig. 2, and also in figs. 18–21, originate at the posterior ends of the buccal folds, and passing beneath the large pump-

* These terms are used for convenience in description, and are not necessarily homologous with the arms of the tentorium as described by Comstock (1902) in insects generally.

muscle, *p.m.*, they become continuous at their proximal ends, by means of thinner chitin, with the middle of the transverse plate *.

A narrow curved rod of chitin, *mx.l.*, articulates at the proximal end of each maxillary sclerite, where that structure fuses with the general wall of the fore-head, and near the base of the mandibular lever on each side. They both pass inwards to become attached to the proximal ends of the internal or ventral stylets (maxillary stylets), and thus form the *maxillary levers, mx.l.*, figs. 2, 3, and 17.

### C. *The Labium.*

The *proboscis* or *labium* (*lbm.*) is formed by an evagination of the integument at the infra-posterior end of the head. In repose it lies closely adpressed against the ventral surface of the body, between the coxæ, and extends for some distance beyond the third pair. It consists of three segments, text-fig. 2, a long proximal segment and two shorter distal segments. Its dorsal or anterior face is folded to form a median, longitudinal groove, which extends along the greater part of its length. At the extremity of the distal article the walls of the fold close completely over, thus forming a short tube, but throughout the rest of its length the groove is open. The proximal end of the proboscis is composed of thin, flexible chitin, as is shown in fig. 1. It is this part which is capable of being drawn into the body during feeding, as will be explained later. This proximal end is not grooved. When specimens are examined, the stylets are usually found lying in the proboscis groove, being held in it by the short, closed tube at its extremity. They are often found extending through the end of this tube, beyond the tip of the proboscis. The distal article of the proboscis bears on its extremity a ring of tactile hairs. During feeding, the proboscis is raised from the surface of the body, and its anterior face is closely pressed against the hypopharynx and maxillary processes.

### D. *The Pharynx.*

The *pharynx* (*ph.*) extends through the head in the median line, and passing over the transverse plate of the tentorium, leads into the œsophagus, fig. 1.

When a cleared potash preparation of the head is examined from the dorsal aspect, two conspicuous prominences are seen at the anterior end of the pharynx. These are the *pharynx protuberances, p.p.*, figs. 12, 13. They are the "Näroiden" described by Dreyfus (1894) in *Phylloxera*. It is in

* Mordwilko (1895) has described these rods in *Lachnus*, as the "Chitinfortsatzestabchen." He considers they are free at their proximal ends. By means of serial sections I have traced these rods in *Schizoneura* to the transverse plate to which they are attached by thin chitin.

this region that the stout pharyngeal struts and the thick, internal walls of the hypopharynx meet, thus forming a firm support for the pharynx.

The pharynx proper (*i. e.*, the part which exerts the sucking force) begins here, and as is seen in the transverse sections, figs. 12–22, the dorsal wall is composed of thin flexible chitin, which is acted upon by large *divaricator muscles*, *d.m.* Anterior to the pharynx protuberances the continuation of the pharynx dips down, and its walls are entirely composed of very stout, rigid chitin, figs. 7–11. The thick chitinous upper wall is formed by the *epipharynx*, *e.p.*, and the lower wall by the *hypopharynx*. This portion does not exert any sucking action, and is simply a duct, *the pharyngeal duct*, *ph.d.*, which conveys the plant-juices into the pharynx proper. This duct, as will be shown later, leads directly into the suction-canal formed by the approximation of the maxillary stylets. The pharynx proper extends from the position of the pharynx protuberances to the transverse chitinous plate of the endoskeleton. It is concave in section, the thin dorsal wall fitting against the stout ventral wall, and possesses a fairly wide lumen.

The *pharynx protuberances* are two hollow, dome-shaped prominences, formed by the meeting of stout chitinous arms in this region, as shown in figs. 12 and 13. They afford a strong support for the anterior end of the pharynx. The dorsal wall of the pharynx, which is thin and flexible, fits snugly between the protuberances into the deep bay formed by the thick ventral wall. In this region the dorsal wall is acted upon by strong divaricator muscles, *d.m.*, which are attached to a median, vertical tendon, *m.t.* It will thus be seen that when these muscles are relaxed, the upper wall of the pharynx fits closely against the ventral wall between the protuberances and practically occludes the opening into the pharynx, thus acting as a kind of entrance-valve. It seems to me, therefore, that the function of the protuberances is simply to strengthen the anterior end of the pharynx, and to render this valvular action more complete.

The *pharyngeal duct*, which really forms part of the pharynx, can be discussed separately, because its function differs from that of the pharynx proper, in that it exerts no sucking-force, but is simply a conducting-canal through which the plant-juices are conveyed from the suction-canal.

The *pharyngeal duct*, figs. 10 and 11, *ph.d.*, dips down and leads to the extremity of the hypopharynx lip *. Its roof is formed by a specially thick plate of chitin, which also forms the floor of the clypeo-labrum, *cl.l.* This structure is the *epipharynx*, *ep.*, figs. 3 and 7–11.

* The mouth, or oral opening, which is really the entrance from the buccal cavity into the pharynx, may be considered as being here. Owing to the special mode of feeding in Hemiptera however, the food-juices, as will be shown later, really enter at the extremity of the compound maxillary stylet, and pass upwards through a special canal into the pharyngeal duct, so that the actual mouth is situated at the extremity of this stylet.

E. *The Epipharynx.*

When examined in transverse sections, fig. 9, the epipharynx is seen to be deeply grooved on its internal face, affording, towards its distal end, a kind of bay in which the maxillary stylets are snugly fitted.

In cleared preparations of the head, fig. 3, the epipharynx is seen to possess a median row of eight well-formed pores, and these are also seen in median longitudinal sections, figs. 1 and 25. Dreyfus (1894) has figured and described a similar structure in *Phylloxèra*, and calls it the hypopharynx. He has also figured the eight pores, but considers these "pale spots" as small chitinous pegs. It may not be out of place here to emphasize the need of verifying observations made on cleared specimens by means of sections. The danger of misinterpreting deeply-seated chitinous structures from cleared transparent specimens is very great, and serial sections are indispensable if a true interpretation of internal chitinous structures is to be gained.

In longitudinal sections the epipharynx appears as a perforated plate, and is probably the perforated languette described by Bugnion and Popoff (1911), and also by Wedde (1885) in other Hemiptera.

Lying above the anterior end of the pharynx and extending over the pores in the epipharynx is an irregular group of cells, possessing large, deeply-staining nuclei, but cell-walls are not defined, fig. 25, *g.o.*

This structure is found in all sections. Behind the epipharynx it seems to divide into two lobes which extend one on each side of the divaricator muscles. In longitudinal sections taken a little out of the median line, I have found a nerve passing from the two anterior lobes of the supra-œsophageal ganglion to each lobe of this structure.

From its position over the perforated epipharynx this structure would seem to be a *gustatory organ*. An organ in this position has been described by Bugnion and Popoff (1911) in Heteroptera, and also by Wedde (1885), but as far as I am able to see with the sections I have made, the histological structure does not agree with the figure given by the former authors. It certainly does not appear to be a glandular structure. I hope in the near future to make special preparations and sections to show the structure of this organ, which will demand the application of special methods. From indirect evidence it would appear that it is an organ of taste, which enables the aphid to test the nature of the sap drawn into the pharyngeal duct before it enters into the pharynx proper.

That aphids are able to readily appreciate differences in the plant-juices derived from different plants is quite certain from observations I have made this year during the progress of some experiments with *Aphis rumicis*. There is no other organ present which could exert such a function. The tactile hairs at the extremity of the proboscis only serve to enable the aphis to find a suitable tender part of the plant in which to insert its stylets.

I have given a longitudinal section, fig. 25, through the epipharynx, showing the position and structure, so far as I am able at present, of this gustatory organ. The section is not quite median, so that the surrounding chitinous structures are not shown very clearly.

F. *Musculature of the Pharynx.*

The anterior or dorsal wall of the pharynx is acted upon by powerful bands of divaricator muscles, which pull out this flexible dorsal wall, thus greatly increasing the lumen of that structure. In the distal half of the pharynx an upright membrane or tendon, *m.t.*, is attached along the middle of the pharynx-wall, and to this tendon are attached the divaricator muscles, *d.m.*, as is shown in figs. 12–16. The muscles pass from each side of this median tendon in parallel bands, and become attached to the wall of the clypeus, on each side of the median line. The internal face of the clypeus possesses several, small, projecting ridges of chitin, which afford a firm attachment for the muscles. These muscles extend to the clypeus in a slightly posterior direction, so that in transverse sections they are often cut across, as shown in fig. 17.

The muscles attached to the proximal end of the dorsal wall of the pharynx are smaller. They converge towards the post-dorsal wall of the clypeus, becoming inserted on its internal face, near together, on each side of the median line.

In fig. 1, which is a slightly schematized median, longitudinal section through the head, the muscles are cut through obliquely and pass out of the line of section before reaching the clypeus.

Between the pharynx protuberances, the pharynx is narrow in transverse section, figs. 12 and 13, and "U"-shaped. When the divaricator muscles are relaxed, the flexible dorsal wall becomes closely adpressed against the ventral wall, completely closing the lumen.

G. *The Salivary Pump.*

The *salivary pump* is a bell-shaped chitinous structure situated below the anterior end of the pharynx, being attached to the hypopharynx, *vide* fig. 2.

In longitudinal section, *vide* fig. 1, it is seen to consist of a stout chitinous distal portion, forming the handle of the bell. This is the *pump-stem, p.s.* It widens out at its proximal end to form a cup-shaped portion—the body of the bell—which is the *pump-cylinder, p.c.* These parts are perhaps better shown in vertical section, fig. 23.

The *pump-cylinder* is a thick-walled, cup-like structure, composed of thick chitin which encloses the *pump-chamber, p.ch.*

The proximal wall of the cylinder consists of membranous chitin, which is continuous with the thick rim of the cup. This wall is usually seen withdrawn into the cylinder, so that only a small part of the chamber remains showing. Attached to this proximal wall is a small club-like tendon to which the large pump-muscle, *p.m.*, is attached. This muscle when it contracts pulls out the proximal wall, thus enlarging the pump-chamber, but in sections the muscle is always seen in the relaxed condition and the pump-chamber is considerably reduced in size, and difficult to see.

The *pump-stem* is attached at its distal end to the wall of the hypopharynx. It is compressed laterally, figs. 12–13. Two strong arms of chitin extend from it laterally and fuse with the lateral walls of the hypopharynx, thus affording a firmer support for the pump.

A minute canal (figs. 12 and 13, *s.ed.*), the *efferent salivary canal*, extends through the dorsal part of the pump-stem, along which the saliva is conducted into the *ejector canal*, *e.c.*, formed by the junction of the maxillary stylets.

The *efferent salivary canal* is continued beyond the pump-stem along the ventral wall of the small hypopharynx lip, being enclosed by this wall, and extends to its pointed extremity (figs. 1 and 10–13, *s.ed.*), where it is continued into a small chitinous process. A similar process extends from the dorsal wall of the lip. There is thus formed a "V"-shaped cleft at the extremity of this structure, as is shown in fig. 25. As will be shown later, the dorsal process forms the continuation of the pharyngeal canal, which leads into the suction canal formed by the maxillary stylets. Similarly the ventral process enclosing the efferent salivary canal leads into the ventral or ejector canal formed by the maxillary stylets.

The *salivary glands** are situated above the œsophagus, and lie obliquely partly in the prothorax and partly in the posterior region of the head, one pair on each side of the median line. The *salivary duct* from each pair passes beneath the thoracic ganglia, and both meet in the median line at the infra-posterior region of the fore-head, where they form a bulbous expansion, *c.s.d.*

From this structure a single *median salivary duct* passes forward into the fore-head. It becomes greatly reduced in size, and extending in the median line beneath the salivary pump, turns upwards, forming an "S"-shaped flexure, and enters the pump-chamber at the post-ventral end of the pump-cylinder, as is shown in fig. 1.

At the place of entry of the salivary duct into the pump-chamber, the walls are so arranged that they exert a valve-like action, the opening being controlled by two small bands of muscles, the *ventral pump-muscles*, *v.m.*, figs. 1 & 2, and figs. 15–18. These muscles are attached, close together, to the wall at the place of entry, and extend backwards below the large pump-muscle, becoming attached to the ventral rods of chitin. The lumen of the salivary duct is extremely small.

The exit opening from the pump-chamber is situated at the antero-dorsal end of the cylinder (fig. 1), and leads into the *efferent salivary canal*, described above as passing through the pump-stem.

* For further description of the salivary glands see Quart. Journ. Micr. Sci. vol. lviii. (1913) p. 680.

H. *Musculature of the Salivary Pump.*

The structure of the salivary pump is such that it acts as a force-pump, the working of which is controlled by the large spindle-shaped *pump-muscle* shown in fig. 1 and fig. 2, *p.m.*

The pump-muscle is attached to the flexible, proximal wall of the cylinder and extends beneath the pharynx, towards the transverse plate of the tentorium, being partly attached to the latter structure and partly to the stout ventral wall of the pharynx. It is divided for some distance along its length, as is seen in transverse sections. The musculature will be considered in more detail later.

I. *The Stylets.*

The *stylets* are situated below the pharynx, and consist of two anterior or dorsal stylets, the *mandibles* (*m.d.*, fig. 3), and two posterior or ventral stylets, the *maxillary stylets* (*mx.s.*, fig. 2).

They are withdrawn for some distance into the fore-head, being swollen in a club-shaped manner at their proximal ends. Distally they become considerably reduced in size, and form long, needle-like structures which, passing through the buccal cavity, extend along the longitudinal proboscis groove. They are finely pointed at their distal extremities, *vide* fig. 24.

The stylets are hollow chitinous structures, which are continuous with the integument of the posterior end of the buccal cavity, being drawn inwards somewhat after the manner of an inverted finger of a glove, *vide* fig. 23. The cavity of the stylet-shaft is especially large in the swollen, proximal part. From the proximal end of each emerges the retort-shaped organ indicated in the series of transverse sections, *md.o.*, *mx.o.*

The relation of the stylets to other structures in the fore-head will be best understood from the serial sections, figs. 4–18.

*The maxillary stylets.*

The *maxillary stylets* lie ventral to the mandibles, one on each side of the median line, and are situated further back. As they emerge into the buccal cavity they approximate towards each other, becoming considerably reduced in size. As is seen in fig. 23, the integument of the buccal cavity, which in this region is thin and membranous, is continued proximally along the shaft of the stylets, forming a sheath in which those structures are freely moveable.

As the maxillary stylets enter the buccal cavity they lie one on each side, along the internal lateral walls of the hypopharynx (fig. 15), fitting into a longitudinally running bay or groove.

Running along the internal face of both stylets is a median longitudinal ridge. This causes two longitudinal grooves to be formed, a dorsal and a ventral groove.

As the stylets extend towards the extremity of the hypopharynx lip, they gradually approach towards the median line, the longitudinal ridge and the two grooves on the internal face becoming more pronounced. At the extremity of the hypopharynx lip they meet in the median line, and the two internal faces become apposed. There is thus formed between the stylets two longitudinal canals (figs. 8 and 9) which are more or less separated by the close apposition of the two longitudinal ridges formed on the internal faces.

I have mentioned before that the tip of the hypopharynx lip possesses a "V"-shaped cleft, owing to the slight prolongation of the two processes which support the openings into the pharyngeal duct and efferent salivary canal. As will be seen in fig. 9, the longitudinal ridges on the internal faces of the maxillary stylets fit into this "V"-shaped cleft, and the dorsal and ventral canals formed by the junction of these stylets enclose the two processes, thus establishing direct communication with the two canals and the pharyngeal duct and efferent salivary canal respectively.

The maxillary stylets do not actually fuse when they meet, but towards their extremity they appear to do so, although the line of fusion is clearly marked.

The compound stylet thus formed possesses two well-marked canals, which run throughout its length :—The dorsal *suction-canal, s.c.*, which conveys the plant-juices to the pharyngeal duct, and thus into the pharynx and a ventral canal. The ventral canal is slightly smaller : it is the *salivary ejector canal, e.c.*, and conveys the saliva from the efferent salivary duct into the tissues of the plant.

Beyond the extremity of the hypopharynx lip, the compound maxillary stylet is supported above in a deep groove on the ventral face of the epipharynx, and below, by grooves on the internal walls of the maxillary sclerites. As is seen in figs. 7, 8, and 9, these surfaces are so arranged that the stylet fits snugly into the grooves, being held firmly in position, at the same time having perfect freedom of movement for protraction or retraction.

Beyond the region of the epipharynx the maxillary processes and the labrum—which is grooved on its ventral face—afford a firm support for the stylets.

Towards the extremity of the labrum the compound stylet enters into the longitudinal proboscis-groove and extends along it to the extremity of the proboscis.

*The maxillary levers.*

The *maxillary levers* are two curved rods of chitin which articulate one at the proximal end of each maxillary sclerite ; each passes into the fore-head, beneath the maxillary stylets (figs. 2 & 3, *mx.l.*, and fig. 17), to the swollen proximal ends of which they become attached, thus affording moveable supporting levers for those structures. The levers project a little way beyond the internal face of the stylets, as shown in figs. 2 and 18, and thus afford attachment for some of the retractor muscle-bands, *mx'.re.*

*The mandibles.*

The anterior stylets are the *mandibles.* They lie dorsal to the maxillary stylets, being disposed slightly further from the median line (fig. 3, *md.*). Although slightly longer, they resemble the latter in general appearance, but remain separate throughout. As they enter the buccal cavity they approximate towards the median line, and extend above the maxillary stylets along the internal walls of the hypopharynx (*vide* figs. 4–14).

Towards the extremity of this structure the internal faces of the mandibles are somewhat concave, and fit closely against its lateral walls. Beyond the junction of the maxillary stylets the mandibles lie by the side of the compound stylet, the internal concave faces of the former closely fitting against the convex outer faces of the latter. They then extend by the side of this stylet along the proboscis-groove.

*The mandibular levers.*

The mandibles are supported by two stout arms of chitin (*md.l.*, fig. 3), which extend, one on each side of the fore-head, from the proximal end of the maxillary fold (fig. 16). They are much stronger than the maxillary levers. Each passes to the base of the mandibles, to which they become attached.

J. *Musculature of the Stylets.*

The mandibles and maxillary stylets can be protracted or retracted by a system of protractor and retractor muscles.

The *retractor muscles of the mandibles* are inserted on the internal face, at the proximal end of those structures (fig. 3, *md.re.*, and figs. 16–21), and extending backwards into the head, divide into two groups, one group becoming inserted along the antero-dorsal arms of the tentorium, the other on the transverse plate of chitin, at the base of these arms.

The *protractor muscles, md.pr.*, are inserted along the base of the mandibular lever, and pass forwards to become inserted along the pharyngeal struts.

The *retractor muscles of the maxillary stylets* (fig. 2, and figs. 18–21, *mx.re.*) consist of two groups of muscles. One group is inserted on the internal face of the proximal extremity of each stylet *, and passing backwards through the head they become attached to the antero-ventral arms of the tentorium, at the base of those structures where they join the transverse plate.

The other group of muscles is smaller, and is attached to the projecting portion of the maxillary lever. The muscles from each lever extend laterally through the head to become inserted on the antero-ventral arms of the tentorium, at the place where that structure bends into the fore-head, *vide* figs. 2 and 18, *mx'.re.*

The large *protractor muscles of the maxillary stylets* are inserted along the external face of the prolonged base of each stylet, and extend in an anterior direction to become inserted on the walls of the maxillary sclerites (fig. 23, *mx.pr.*).

K. *Musculature of the Head.*

I have shown that the fore-head freely articulates with the proximal portion of the head by means of a membranous chitinous fold. This allows the fore-head to be raised from the deflexed position it occupies in repose, to a position more or less at an angle to the body, which it occupies when the aphis is feeding. These movements are brought about by two sets of muscles, the *elevator muscles* of the fore-head and the *depressor muscles.*

Extending from the transverse plate of chitin are two bands of muscles which pass through the proximal portion of the head, in a postero-lateral direction, and become inserted on the post-lateral border of the head, at its junction with the prothorax. These muscles are not shown in fig. 1, as they are attached at the ends of the transverse plate, and are not seen in median section. I have indicated them in the schematic text-figure 2, *m.d.p.* When these muscles contract they pull down the transverse plate of the tentorium, and as this structure, by means of the tentorial arms, is firmly attached to the fore-head, this latter structure is elevated from its deflexed position. I call these muscles therefore, the *elevator muscles of the fore-head.*

The *depressor muscles of the fore-head* consist of two strong muscles which are attached, in the median line, to the floor of that structure (figs. 18 & 19, *m.d.f.*). They diverge laterally, in a slightly posterior direction, and become inserted on the antero-ventral arms of the tentorium. When the aphis has

* Muir and Kershaw (1912) consider that the part of the stylets projecting into the head and supporting the retractor and protractor muscles are chitinized tendons originating "by the invagination of the ectoderm at the base of the setæ, which becomes solid, or partly solid, by deposits of chitin." As may be seen in fig. 23, the maxillary stylets are apparently continued for some little distance into the head, thus affording attachment for the muscles. This part is chitinous, and in the case of the mandibles the chitin possesses small chitinous papillæ, which afford firm attachment for the retractor muscles. The base of the stylets seems to be continued into the head for a short distance beyond the continuation of the integument of the buccal cavity, thus affording an attachment for the muscles.

finished feeding, and these muscles contract, the fore-head is pulled back into the normal deflexed position.

There are two other bands of muscles attached to the ends of the transverse plate of chitin (text-fig. 2, *m.e.p.*). They extend through the head, almost parallel, in a plane continuous with that of the large pump-muscle, and are inserted on the wall of the head. These are the *elevator muscles oj the transverse plate*. From their position the function undoubtedly is to counteract the pull on this structure, of the large pump-muscle and the retractor muscles of the stylets.

I have shown that the salivary pump is held firmly in position by chitinous supports. When the large pump-muscle contracts, thus operating on the proximal wall of the pump-cylinder, there must be also a considerable pull on the transverse plate, and if this structure were allowed to be pulled in the direction of the pump, the muscle would be deprived of a considerable amount of its force exerted on the pump. This is overcome by the action of the elevator muscles of the transverse plate. When these muscles contract they exert a pull along the same plane as the pump-muscle, but in the opposite direction.

L. *How Suction is accomplished.*

I have indicated when describing the anatomy of the mouth-parts how the plant-juices are conveyed into the pharynx, and how the saliva is conveyed into the plant-tissues.

I shall now give a concise account of the way it seems to me the mouth-parts work during the operation of feeding.

Owing to the minute structure concerned it has not been possible to work the parts experimentally, or to observe them working in the living insect, so that the following conclusions have been arrived at by means of a careful study of the anatomy, and especially the distribution of the muscles.

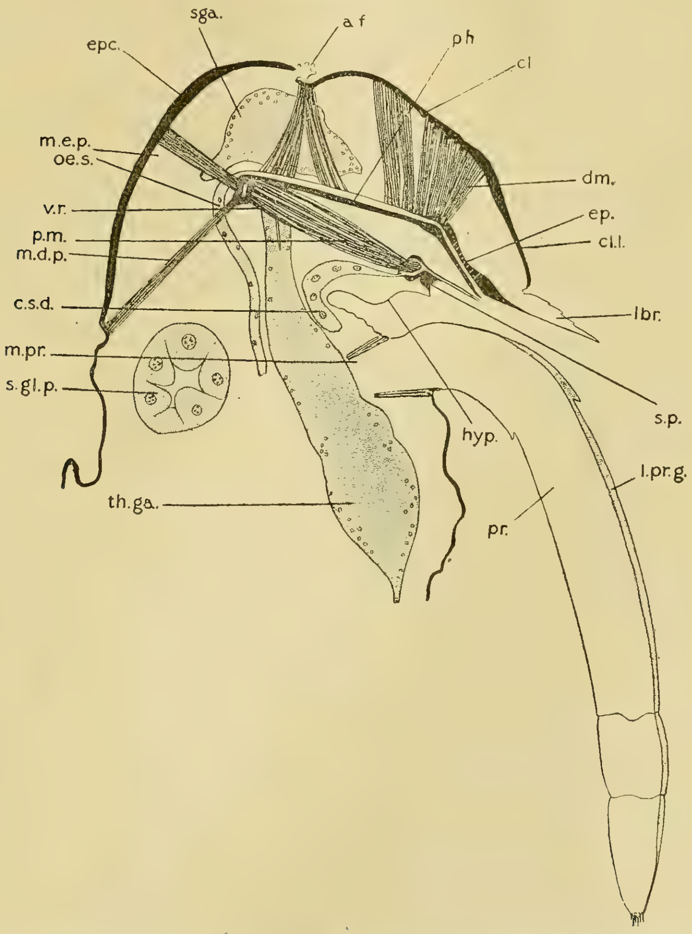
The proboscis is raised from the body, and a suitable part of the plant-host is selected in which to insert the stylets. The distal article of the proboscis is freely moveable, and exerts a tactile function by means of the tactile hairs on its extremity.

The fore-head is also raised from its deflexed position by the contraction of the two elevator muscles of the fore-head (*m.d.p.*). The stylets lie along the longitudinal groove on the anterior face of the labium, to which the labrum is closely adpressed.

The fore-head and proboscis are now in the position for the working of the stylets.

By means of the large protractor muscles (fig. 23, *mx.pr.*), the compound maxillary stylet is forced into the tissues of the plant. This stylet, as has been described above, is held firmly in position by the deep grooves on the internal face of the epipharynx and labrum and the grooves on the internal walls of the maxillary sclerites. Proximally, before they come together, the two maxillary stylets work smoothly along the internal walls of the hypopharynx. As they lie along the proboscis-groove, they are held in position at the extremity of the proboscis by the folding over of the walls of the groove, which thus forms a tube through which the stylets pass into the plant.

Text-fig. 2.




Schematic longitudinal section through the head, showing relation of parts. × 160. The stylets have not been shown, in order to avoid confusion. The working of these structures will be readily understood from figs. 2 and 3.

At the same time the large protractor muscles of the mandibles (*md.pr.*) contract, and pull down the mandibular levers, so that the mandibles are also forced into the plant *.

* From examination of some sections of plant tissues with the stylets in position (*Aphis rumicis* on *Chenopodium album*), the stylets were found to pass between the cortical cells in a more or less irregular course to the vascular bundles.

During the insertion of the stylets, the proximal part of the proboscis is withdrawn into the body by the protractor muscles (*m.pr.*). This enables the stylets to be forced deeper into the tissues of the plant ; at the same time they are strengthened by being supported outside the plant in the proboscis-groove. I have indicated above, that the proximal end of the proboscis is very thin and membranous, which allows it to be readily retracted.

The mandibles remain free throughout, although they are closely apposed to the compound maxillary stylet, and strengthen this structure during the piercing of the plant-tissues.

When the stylets have been forced into the desired part of the plant-tissues, suction commences.

Owing to the very minute lumen composing the suction-canal, *s.c.*, it is very probable that the plant-juices ascend up this canal, largely by means of capillarity, and there is the further factor of the pressure of the sap itself.

As the divaricator muscles of the pharynx contract, they pull out the flexible, dorsal wall of the pharynx, thus greatly enlarging the lumen of that structure. This causes a sucking action, and as the plant-juices make their way from the suction-canal up the pharyngeal duct, they are drawn from the latter duct into the pharynx proper.

The divaricator muscles acting on the posterior half of the pharynx are not so strong as those acting on the anterior half. I have shown that the stout, ventral wall of the pharynx between the pharynx protuberances is deeply concave, so that when the divaricator muscles of this part are relaxed the dorsal wall becomes adpressed to the ventral wall and practically occludes the entrance from the pharyngeal duct. As the other divaricator muscles are relaxed the dorsal wall tends to regain its original position by virtue of its own elasticity, and as a result, the lumen being considerably reduced in size, the juices are forced backwards into the œsophagus, and thus into the stomach. At the entrance of the œsophagus into the stomach, there is formed a well-defined œsophageal valve, which prevents regurgitation of the food into the pharynx *.

The working of the salivary pump is produced by the large pump-muscle, *p.m.* When this muscle contracts, the proximal wall of the pump-cylinder is pulled out (fig. 23), thus enlarging the lumen of the pump-chamber. By the contraction of the small ventral muscles, fig. 25, *v.m.*, the entrance from the median salivary duct into the pump-chamber is opened and the saliva passes into the pump-chamber.

It will be noticed in fig. 23 that the thick proximal rim of the pump-cylinder, which is slightly inturned, is also pulled out, and the strong walls of that structure are thus forced outwards, which is rendered possible by the elasticity of the thick chitin. It is for this reason that the pump-muscle is

* Davidson, J., Quart. Journ. Micr. Sci. vol. lviii. (1913) p. 680.

so powerful, as the force required to squeeze out the walls of the cylinder must be very considerable. The resulting pull on the transverse plate of the tentorium must be very great, and to counteract this there are the two elevator muscles of that structure, *m.e.p.* These muscles exert a pull in the same plane as the pump-muscle, but in the opposite direction.

If the only function of the pump-muscle were to pull out the flexible proximal wall such great force would not be needed. Further, it is very improbable that the return of this wall would give sufficient force to propel the saliva from the pump-chamber, along the minute efferent salivary canal, and then down the ejector canal formed between the maxillary stylets.

When the saliva has collected in the pump-chamber the small ventral muscles (*v.m.*) are relaxed and the opening from the median salivary duct (afferent canal) is closed. The large pump-muscle is then relaxed and the walls of the pump-chamber return to their normal position. The force of the contracting walls of the cylinder is such that the saliva is forced into the efferent canal, down into the ejector canal. The flexible proximal wall of the cylinder gradually returns to its normal position and the cavity of the chamber is considerably reduced in size, the contents being forced down the salivary ejector canal into the tissues of the plant at the extremity of the compound maxillary stylet as explained above. When the chamber is emptied, the process is repeated as before.

As regards the function of the saliva I am not able at present to say anything definite. Meek (1903) remarks that the saliva of Hemiptera is alkaline, and has the power of changing starch into sugar. He refers to the work of Plateau (1874), 'Recherches sur les Phénonomène de la Digestion chez les Insectes,' who holds that primarily the saliva serves as a digestive fluid.

It may be, considering the extreme minuteness of the suction canal, that the ascent of the cell-sap along this canal is largely due to capillarity, and that the addition of the saliva causes the surface-tension of the sap to be lowered, thus facilitating its ascent up the suction-canal.

When suction is finished the pump-muscles and the protractor muscles of the stylets are relaxed, the stylets being withdrawn from the tissues of the plant by the contraction of the retractor muscles *md.re.*, *mx.re.* The integument at the posterior end of the buccal cavity is thin and flexible, thus allowing the stylets to be withdrawn for some distance into the head, into a kind of integumental sheath. The pull exerted on the tentorial arms by the retractor muscles is largely counteracted by the two elevator muscles of the transverse plate.

When the stylets are withdrawn from the plant the proboscis muscles are relaxed and that structure returns to its normal position of repose. Similarly the depressor muscles of the head pull the fore-head into its normal deflexed position.

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## EXPLANATION OF THE PLATES.

### *Reference lettering.*

*a.d.* Antero-dorsal arms of the tentorium.
*a.v.* Antero-ventral arms of the tentorium.
*a.f.* Thin chitinous fold joining fore-head to epicranium.
*ant.* Antenna.
*b.c.* Buccal cavity.
*b.f.* Buccal fold.
*c.ep.* Stout chitinous mass formed at the beginning of the pharynx by junction of clypeal folds and internal walls of hypopharynx.
*c.s.d.* Common median salivary duct.
*cl.* Clypeus.
*cl.f.* Clypeal fold.
*cl.l.* Clypeo-labrum.
*cl.sc.* Clypeal sclerite.
*conn.* Œsophageal connective joining supra- and sub-œsophageal ganglia.
*d.m.* Divaricator muscles of pharynx.
*e.c.* Ejector canal (salivary) formed by meeting of maxillary stylets.
*epc.* Proximal part of head (epicranium).
*ep.* Epipharynx.
*ep.gr.* Longitudinal groove on epipharynx.
*f.h.* Ventral wall or floor of fore-head.
*f.b.* Fat-body cells.
*g.o.* Gustatory organ.
*hs.* Hypodermis.
*hyp.* Hypopharynx.
*hyp.l.* Hypopharynx lip.
*lbr.* Labrum.
*lbm.* Labium.
*lbr.g.* Longitudinal groove on labrum.
*l.pr.g.* Longitudinal groove on proboscis.
*l.w.* Thin post-lateral walls of head.
*md.* Mandibles.
*md.l.* Mandibular lever.
*md.pr.* Protractor muscles of mandibles.
*md.re.* Retractor muscles of mandibles, attached to antero-dorsal arms.
*md'.re.* Retractor muscles of mandibles, attached to transverse plate.
*m.d.f.* Depressor muscles of fore-head.
*m.d.p.* Elevator muscles of fore-head.
*md.o.* Retort-shaped organs of mandibles.
*mx.s.* Maxillary stylets.
*mx.re.* Retractor muscles of maxillary stylets, attached to transverse plate.
*mx'.re.* Retractor muscles of maxillary stylets, attached to antero-ventral arms.
*mx.p.* Maxillary processes.
*mx.sc.* Maxillary sclerite.
*mx.l.* Maxillary lever.
*mx.f.* Maxillary folds.
*mx.sh.* Integument of buccal cavity forming a sheath round stylets.
*mx.o.* Retort-shaped organs of maxillary stylets.
*mx.pr.* Protractor muscles of maxillary stylets.
*m.t.* Median vertical tendon to which the divaricator pharyngeal muscles are attached.
*m.e.p.* Elevator muscles of transverse plate.
*œs.* Œsophagus.
*p.c.* Pump-cylinder enclosing pump-chamber.
*p.ch.* Pump-chamber.
*p.m.* Pump-muscle.
*p.w.* Post-dorsal wall of clypeus (fore-head).
*p.p.* Pharynx protuberances.
*p.v.w.* Post-ventral border of fore-head.
*ph.* Pharynx.
*ph.d.* Pharyngeal duct leading from the suction-canal into pharynx proper.
*ph.o.* End of pharynx and beginning of œsophagus.
*pr.w.* Flexible proximal wall of labium.
*pr.* Labium (proboscis).
*p.s.* Pump-stem.

*pst.* Insertion of pump-muscle on the flexible proximal wall of salivary pump.

*s.ga.* Supra-œsophageal ganglion.

*s.c.* Suction-canal formed between the maxillary stylets and leading into pharyngeal duct.

*s.e.d.* Efferent salivary duct leading from salivary chamber into the salivary ejector-canal formed between the maxillary stylets.

*s.p.* Salivary pump.

*s.gl.p.* Posterior salivary gland.

*t.p.* Transverse chitinous plate of endoskeleton.

*th.ga.* Thoracic ganglia.

*v.r.* Ventral rods of chitin extending from posterior angles of the buccal folds.

*v.m.* Small ventral muscles of salivary pump, which act on the opening of the salivary duct into the pump-chamber.

## Plate 24.

Fig. 1. Median longitudinal section through the head, slightly schematised, showing salivary pump, pharynx, etc. × 600. The indicating lines at the side indicate the plane through which the transverse serial sections figs. 4–22 have passed; the numbers refer to the number of the transverse section given. Figure drawn in outline from longitudinal section with Camera lucida.

2. Fore-head, ventral view, showing stylets, musculature, etc.—*Note.* The maxillary sclerites really come close together in the median line over the hypopharynx lip, but they are shown displaced from the median line so as to show the underlying hypopharynx lip. The lines at the side indicate the plane of the serial sections as in fig. 1. Figure drawn from potash preparation.

3. Fore-head, dorsal view, showing mandibles, musculature, and endoskeleton. Side-lines indicate as in fig. 1. Figure drawn from cleared preparation. The length is increased slightly out of proportion so as to show the antero-dorsal arms.

Figs. 4–11. Transverse sections through fore-head (*i. e.* at right angles to its longer axis), in planes indicated by side-lines in figs. 1–3. × 1245.

Fig. 23. Vertical section through fore-head, showing salivary pump and maxillary stylets. × 300.

## Plate 25.

Figs. 12–14. Continuation of the same series of transverse sections.

15–22. Transverse sections through fore-head in planes indicated by side-lines in figs. 1–3. Continuation of same series. × 450.

Fig. 24. (*a*) Extremity of compound maxillary stylet, showing two canals. × 1250.

(*b*) Extremity of mandible. × 1250.

25. Longitudinal section, almost median, showing gustatory organ and its relation to perforated epipharynx. Stained with hæmatoxylin and orange G. × 450. The section is not quite median.


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